NeoBiota 90: 53–78 (2024)
doi: 10.3897/neobiota.90.101797
https://neobiota.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

Worldwide distribution and phylogeography of the agave weevil *Scyphophorus acupunctatus* (Coleoptera, Dryophthoridae): the rise of an overlooked invasion

Andrea Viviano[1,2], Arturo Cocco[3], Paolo Colangelo[4,5], Giuseppe Marco Delitala[6], Roberto Antonio Pantaleoni[1,3], Laura Loru[1]

1 *National Research Council (CNR), Institute of Research on Terrestrial Ecosystems (IRET), trav. La Crucca 3, Baldinca, 07100 Sassari, Italy* **2** *National Research Council (CNR), Institute of Research on Terrestrial Ecosystems (IRET), via Madonna del Piano 10, 50019 Sesto Fiorentino (Florence), Italy* **3** *Department of Agriculture, University of Sassari, Viale Italia 39, 07100, Sassari, Italy* **4** *National Research Council (CNR), Institute of Research on Terrestrial Ecosystems (IRET), Strada Provinciale 35d 9, 00010 Montelibretti (Rome), Italy* **5** *National Biodiversity Future Center, 90133, Palermo, Italy* **6** *via Claudio Fermi 24, 07100, Sassari, Italy*

Corresponding author: Arturo Cocco (acocco@uniss.it)

Academic editor: Katelyn Faulkner | Received 14 February 2023 | Accepted 6 November 2023 | Published 9 January 2024

Citation: Viviano A, Cocco A, Colangelo P, Delitala GM, Pantaleoni RA, Loru L (2024) Worldwide distribution and phylogeography of the agave weevil *Scyphophorus acupunctatus* (Coleoptera, Dryophthoridae): the rise of an overlooked invasion. NeoBiota 90: 53–78. https://doi.org/10.3897/neobiota.90.101797

Abstract

Global plant trade represents one of the main pathways of introduction for invertebrates, including insects, throughout the world. Non-native insects include some of the most important pests affecting cultivated and ornamental plants worldwide. Defining the origins and updating the distribution of non-native invasive species is pivotal to develop effective strategies to limit their spread. The agave weevil, *Scyphophorus acupunctatus* (Coleoptera, Dryophthoridae), is a curculionid beetle native to Central and North America, although it also occurs in Eurasia, Africa, Oceania and South America as a non-native species. Despite being widespread, the extent of occurrence and origins of European populations of the agave weevil have been overlooked. In the present study, the current and potential worldwide distribution of *S. acupunctatus* was assessed and an analysis of its genetic diversity in the native and non-native ranges was performed. By analysing occurrences from local phytosanitary bulletins and citizen-science platforms, the agave weevil was confirmed to be widely distributed and to occur on all continents, except Antarctica. Additionally, there is potential for expansion throughout the world, as estimated by species distribution models. Nucleotide and haplotype diversity of the COXI mitochondrial gene (about 650 bp) was lower in the non-native (n = 39 samples) than native populations (n = 26 samples). The majority of introduced

Copyright *Andrea Viviano et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

individuals belonged to the same haplotype, suggesting that most introductions in Europe might have occurred from a small geographical area in Central America. Constant transboundary monitoring and national laws must be considered to reduce the spread of the agave weevil, given that a bridgehead effect may occur from non-native populations to new suitable areas.

Keywords

Agave, mitochondrial COXI gene, non-native invasive insects, population genetics, species distribution model

Introduction

Non-native invasive species are taxa that have been introduced and/or spread into regions outside their native ranges and have subsequently established and spread, affecting local ecosystem dynamics (CBD 2010). Since the Holocene and the earliest explorers, human migration has been essential to the movement of species from their native ranges to areas where they were not present (Foster et al. 2002; Banks et al. 2015). Globalisation has intensified the human-assisted spread of living species in non-native areas, following international trade and human journeys (Meyerson and Mooney 2007). In addition, the creation of ecological corridors has facilitated the range expansion of many taxa in non-native countries (Mattson et al. 2007; Horsák et al. 2019).

Crop pests are widely distributed worldwide due to accidental introductions through the intensive trade of goods, including plants of ornamental and agronomic interest (Deutsch et al. 2018). Amongst crop pests, many invertebrate species have been thoroughly studied, particularly in biocontrol and pest management research (Geier 1966; Parsons et al. 2020). Well-studied crop pest species include *Halyomorpha halys* (Stål) and *Tuta absoluta* (Meyrick) (Biondi et al. 2018; Cianferoni et al. 2018). However, most non-native insect pests have been poorly investigated and their impact and distribution are currently still under assessment (e.g. *Corythauma ayyari* (Drake) and *Stator limbatus* (Horn): Mazza et al. (2020); Cocco et al. (2021)). For instance, palms in Mediterranean countries are threatened by both the well-known red palm weevil, *Rhynchophorus ferrugineus* (Olivier) (Soroker and Colazza 2017) and the still mostly unknown and overlooked palm borer moth, *Paysandisia archon* (Burmeister) (Mori et al. 2023). Curculionid coleopterans (e.g. weevils) are an important threat to many cultivated species including corn, figs, palms and other ornamental plants (Guzmàn et al. 2012; Inghilesi et al. 2015; Farina et al. 2020). Amongst those, the agave weevil, *Scyphophorus acupunctatus* Gyllenhal (Coleoptera, Dryophthoridae), is one of the least-studied species. This weevil is native to southern North America, Mexico and other countries in Central America (Vaurie 1971), although it has been introduced to several parts of the world including American islands and South America (US Virgin Islands and Hawaii, Cayman Islands, Puerto Rico, Cuba, Haiti, Jamaica, Dominican Republic, Curaçao, Colombia, Venezuela and Brazil), Africa (Kenya, Tanzania and South Africa), Asia (Indonesia and Saudi Arabia), Oceania (South Australia and Fiji Islands) and Europe (Portugal including Madeira, Spain including Canary and Balearic

Islands, France, Italy, Croatia, Greece and Cyprus: Setliff and Anderson (2011); CABI/EPPO (2014); Vassiliou and Kitsis (2015); Andrade (2022); Pernek and Cvetković (2022)). Populations of *S. acupunctatus* in Central America (Honduras, Belize, Guatemala, Costa Rica, El Salvador and Nicaragua) have an uncertain origin, as it is unclear whether they are native or not. These populations may represent an undocumented natural range expansion from northern countries, i.e. Mexico, in recent times or they might have been introduced through plant and horticultural trade (Vassiliou and Kitsis 2015; EPPO 2022a). Occurrences of the agave weevil in Israel, New Zealand, Queensland (Australia), Argentina and the United Kingdom that have been reported by some authors (CABI 2023), have never been confirmed in the scientific literature, nor in citizen-science platforms or social networks. In general, the distribution of this weevil is mainly known at the country level, with little known about its actual distribution within each country (Martín-Taboada et al. 2019).

The agave weevil is a major pest of agave. Agaves (Asparagaceae, Agavoideae/Agavaceae) include several genera and species that have been introduced worldwide for ornamental purposes (Thiede et al. 2019). Most agave species are susceptible to this weevil, particularly those belonging to the genus *Agave* (Vaurie 1971; Bolaños et al. 2014; Palemòn-Alberto et al. 2022). Plants are directly damaged by the agave weevil whose larvae feed on agave heads by boring galleries (Figueroa-Castro et al. 2016). The consumption of plant parts by the agave weevil larva may cause plant mortality (Aquino-Bolaños et al. 2013). Adults cause little damage in comparison to larvae.

The taxonomy of the *Scyphophorus* genus is still unresolved (Chamorro et al. 2016). Although two species are traditionally recognised, *S. acupunctatus* and *S. yuccae* Horn, no reliable information on the phylogeography of this genus is available. Genetic analyses of *Scyphophorus* spp. have been carried out on a limited sample size or in limited geographical areas of Central America (Azuara-Domínguez et al. 2013; Chamorro et al. 2016). Furthermore, no molecular data are available to disentangle the two *Scyphophorus* species, given that the only deposited sequence of *S. yuccae* is actually belonging to *S. acupunctatus*, questioning the actual validity of the former species (Chamorro et al. 2016). Assessing the geographic origin of non-native populations of *S. acupunctatus* may help to provide information for plant trade controls and assist with preventing new invasions. Although *S. acupunctatus* is also recorded in Africa, SE Asia and Australia, most non-native populations of this weevil occur in Europe, where *S. acupunctatus* has been introduced through the plant trade (e.g. *Beaucarnea recurvata* Lem., *Agave americana* L. and *Yucca* spp.), most likely from different countries of Central and North America (e.g. from Nicaragua to Italy: EPPO (2022b)). The agave weevil was reported for the first time in the Netherlands in 1980 (van Rossem et al. 1981) and, subsequently, in Italy, France, Spain and Greece (Colombo 2000; Flinch and Alonso-Zarazaga 2007; EPPO 2008; Kontodimas and Kallinikou 2010). Therefore, we focused mostly on European and Mediterranean countries, as these countries include most of the non-native range of this weevil species.

The aims of our work were to: (*i*) update the distribution of the agave weevil in non-native areas with special regard to Mediterranean countries; (*ii*) determine the climatic

suitability throughout the world, with special regard to Europe, where most non-native populations occur and predict its potential distribution; and (*iii*) assess the phylogeographic pattern of *S. acupunctatus* and trace the origin of European populations.

Materials and methods

Updating the distribution of the agave weevil

The distribution of the agave weevil in its non-native range was updated by searching for published and unpublished records in the grey and scientific literature and online databases, including records collected through citizen-science and validated by experts (i.e. iNaturalist: www.inaturalist.org; GBIF: www.gbif.org DOI: https://doi.org/10.15468/dl.pd22mh; Forum Natura Mediterraneo: www.naturamediterraneo.com; Forum Entomologi Italiani: www.entomologiitaliani.net. All accessed on 15.05.2023). The search for occurrence records was conducted from October 2022 to May 2023. Further searches were performed on free posts with photos on Social Networks (e.g. Facebook) and on video-sharing websites (e.g. YouTube). The literature search was carried out by assessing studies in online databases (i.e. ISI Web of Science, Scopus, Zoological Records and Google Scholar). Search terms included all possible combinations of the words: 'agave weevil', '*Scyphophorus acupunctatus*', 'distribution' and 'non-native species'. The same words were searched in English, French, Spanish, Portuguese and Italian. Maps representing the agave weevil distribution using geographical coordinates were downloaded from the ESRI (https://server.arcgisonline.com) and Eurostat (Countries – GISCO – Eurostat, europa.eu) websites. The distribution of the weevil was mapped using QGIS software version 3.28 Firenze (QGIS Development Team 2019).

The suitability of current and future climates for the agave weevil: preliminary analyses

The potential worldwide distribution of *S. acupunctatus* was modelled to identify areas throughout the Globe that are climatically suitable for this weevil. To the best of our knowledge, no previous studies have focused on the climatic preferences of this weevil, despite its high impact on agro-economy and urban parks.

Occurrence records from both the native and non-native ranges were collected, representing the whole realised ecological niche (Srivastava et al. 2021). This approach resulted in a total of 1525 high-accuracy occurrence records (uncertainty < 1 km). The raw dataset underwent a meticulous analysis to identify and eliminate duplicate entries. This process was carried out in two steps: an initial manual inspection employing the duplicate search function in Microsoft Excel (Microsoft Office 365), followed by subsequent verification using the "duplicated" function of "spocc" package (Chamberlain et al. 2017) in the R software version 4.1.2 (R Core Team 2019). By implementing these measures, overlapping data points from various sources were successfully identified and removed. A final new dataset of 1135 occurrences without duplicates was obtained.

Moran's correlograms were employed to test for the presence of significant spatial autocorrelation (De Marco et al. 2008), using spatial analysis tools available in ArcGIS Pro (ESRI 2011). The spatial autocorrelation analysis was conducted using the final dataset as the input file. In detail, we assessed the spatial autocorrelation between 1 and 10 km at 1 km intervals (De Marco et al. 2008; Crase et al. 2014).

The Moran's correlogram is a graphical representation of the spatial autocorrelation coefficient (Moran's I) at different distance intervals, which helps to identify patterns of spatial dependence and assess whether neighbouring observations are more similar or dissimilar from each other than expected by chance (Crase et al. 2014). The Moran's I coefficient ranges from -1 to 1, where positive values indicate positive spatial autocorrelation (similar values tend to cluster together), negative values indicate negative spatial autocorrelation (dissimilar values tend to be clustered) and values close to zero indicate no spatial autocorrelation (values are randomly distributed across space: Crase et al. (2014), Suppl. material 1: fig. S1).

In this work, the computed Moran's Index was 0.03, indicating a slight positive spatial autocorrelation in the dataset. The Z-score, which measures the standard deviation from the expected mean under the assumption of spatial randomness, was 0.18. The associated P-value was 0.86, suggesting that the observed spatial pattern was not significantly different from what would be expected by chance. Overall, these findings suggested the absence of significant spatial clustering or dispersion in the analysed spatial context. The final dataset used in the model consisted of 718 occurrences.

A distance threshold of 10 km was set to define spatial relationships between observations. This threshold represents the maximum distance at which observations are spatially related. The analysis was performed without any specific selection set, meaning that all observations within the study area were included in the analysis. No weight matrix file was used, suggesting that all observations were assumed to have equal influence in the analysis.

Dispersal abilities of *Scyphophorus* weevils are limited (< 50 metres), as reported by the scientific literature (Huxman et al. 1997; Figueroa-Castro et al. 2016). In line with the spatial autocorrelation analysis, a 10 km distance was selected to filter the occurrences (Di Cola et al. 2017; Montalva et al. 2017; Atauchi et al. 2018; Guevara et al. 2018).

In the final analysis, occurrences were filtered by selecting the minimum distance of 10 km between different occurrence points using the "spThin" R package (Aiello-Lammens et al. 2015). This distance threshold allows for the consideration of occurrences as independent from one another and aligns with the resolution of climate data (Ancillotto et al. 2023).

Selection of variables

The modelling process was started by obtaining 19 climatic variable layers from the Worldclim (version 2.1) website, with a resolution of 2.5 minutes of a degree (Fick and Hijmans 2017). Subsequently, a Principal Component Analysis (PCA: Suppl. material 1: figs S2, S3) was performed using the "ade4" package in R to identify variables with a high collinearity and explore their correlation structure (Fourcade et al. 2014).

Variables were carefully chosen for modelling *S. acupunctatus* by excluding those showing strong intercorrelation. As a result, six highly-significant variables were selected to model the distribution of *S. acupunctatus* (Suppl. material 1: table S1). These variables included BIO1 (Annual Mean Temperature), BIO4 (Temperature Seasonality), BIO6 (Minimum Temperature of the Coldest Month), BIO7 (Temperature Annual Range), BIO9 (Mean Temperature of the Driest Quarter) and BIO11 (Mean Temperature of the Coldest Quarter).

Additionally, the Variance Inflation Factor (VIF) for all selected variables was computed using the "usdm" package in R (Naimi et al. 2014). The VIF values were examined to ensure that all values were below 3, indicating a very low level of multicollinearity (Prakash 2019). Specifically, variables with a Pearson's correlation coefficient of below 0.70 or above -0.70 were retained (Alin 2010; Kock and Lynn 2012; Regos et al. 2020) (Suppl. material 1: table S2). The six bioclimatic variables that were selected to model the distribution of *S. acupunctatus* under current climatic conditions were also chosen to model the distribution of the species under future climates, spanning from 2041 to 2070. Future climate data were downloaded under the Representative Concentration Pathways (RCP 2.6) scenario. The RCP 2.6 future bioclimatic raster is widely acknowledged in literature as a representative case for mitigation strategies aimed at constraining the rise of global mean temperature to 2 °C (van Vuuren et al. 2011).

Algorithm selection

A first comprehensive evaluation was conducted to estimate the performance of nine algorithms through a combination of R packages such as "ENMeval" and "sdm" (Kass et al. 2021; Montoya-Jiménez et al. 2022).

The evaluation encompassed a range of algorithms, namely the Generalised Linear Model (GLM, with a logit-link function), Boosted Regression Trees (BRT, with 15% holdout validation point and bagging fraction set to 0.5: Mui (2015)), Random Forest (RF, with max. tree depth = 2–4: Valavi et al. (2021)), Maximum Entropy (MaxEnt), Generalised Additive Model (GAM), Multivariate Adaptive Regression Splines (MARS), Geometric Brownian Motion (GBM), BIOCLIM and Functional Data Analysis (FDA: Pecchi et al. 2019; Steen et al. 2021). The goal was to identify the most suitable models for the study and reduce computational efforts. To achieve this, along with presence records, 6000 random background points (1000 background points per continental area where the occurrence of *S. acupunctatus* is reported, i.e. North America, South America, Europe, Asia, Africa and Oceania) were generated (Barber et al. 2022; Buonincontri et al. 2023). In particular, background points were selected in a buffer of 10,000 metres around occurrences, in line with previous literature (Iturbide et al. 2015; Rotllan-Puig and Traveset 2021). Evaluation metrics, such as the Area Under the Curve (AUC) and True Skill Statistics (TSS), were employed to assess the model performance (Suppl. material 1: table S3: Steen et al. (2021)). Unsuitable models (AUC < 0.90; TSS < 0.75) were discarded.

Modelling

Species Distribution Models (SDM) were performed using the R packages "biomod2" and "sdm" (Thuiller 2014; Naimi and Araújo 2016). Following the previous evaluation, only the most suitable model algorithms were selected for the inclusion in the ensemble model. The selection process aimed at choosing models with the highest performance to promote accurate forecasts and ensure reliable results (Thuiller 2014). An ensemble species distribution model was fitted using four algorithms: MaxEnt, RF, GLM and GAM (Araujo and New 2007). By incorporating both statistical and machine-learning approaches, the ensemble approach enables a comprehensive analysis and assessment of the species' potential distribution, which cannot be reached with a single-model approach when the performance of the individual models is low (Araújo and New 2007; Buisson et al. 2010; Hao et al. 2019). This integration of different modelling techniques enhances the robustness of the analysis and improves the overall understanding of the studied phenomenon. Amongst the obtained models, the RF performed the best, with an AUC = 0.99 and TSS = 0.90 (Suppl. material 1: table S3).

The results of the models were assembled with a weighted average of all predictions from all fitted models (Buisson et al. 2010; Smith et al. 2017). The variables for future projections (2041–2070) were then downloaded. Future projections of these variables were obtained for the emission-conservative scenario known as RPC 2.6. Built models were then projected under future climatic conditions. The bioclimatic rasters for future climates at a 2.5-minute degree resolution were evaluated following the same procedures described earlier (Ancillotto et al. 2016, 2020; Cancellario et al. 2023). This approach provided valuable insights into the possible impacts of climate change on the climatic suitability of the world for the agave weevil. For the RCP 2.6 scenario and for each variable, the median of five Global Circulation Models (GCMs) was used: GFDL-ESM4, UKESM1-0LL, MPIESM1-2-HR, IPSLCM6A-LR and MRI-ESM2-0 (Mori et al. 2023). Models were validated using spatial cross validation with the R package "blockCV" (Valavi et al. 2019). The K-fold cross validation was performed, with K = 5 as determined through the "buffer evaluation", i.e. by using the function "cv_buffer" (Pohjankukka et al. 2017).

Model performance was measured using TSS and AUC. For present and future projections, an occurrence probability raster was obtained for each statistical model by calculating the mean of all the projections with a TSS > 0.75 and an AUC > 0.90 (Mori et al. 2023).

Then, differences between predictions under future and current climates were obtained using consensus models, by subtracting the average predictions under current climates from those under future climate. Raster cells with positive values indicated a predicted improvement in climatic conditions for *S. acupunctatus*, whereas raster cells with negative values indicated a decreased climatic suitability for the future. To estimate the uncertainty in the predictions due to disagreements amongst four different algorithms, subtraction per model was performed and the following values were assigned: value -1 was assigned to all cells with negative values of the average single-

model predictions; similarly, the value +1 was assigned to all cells with positive values and 0 otherwise (Mori et al. 2023).

The consensus of model predictions was obtained by summing the four three-value maps (-1, 0, 1). A raster map was obtained with values ranging between -4 and +4, with extreme values suggesting that all the four statistical models predicted a decrease (-4) or an increase (+4) in the probability of occurrence, whereas intermediate values indicated a partial (±2; ±3) or high disagreement (-1 to +1) amongst the predictions of the algorithms (Suppl. material 1: fig. S4).

The potential non-analogue climate was checked using a Multivariate Environmental Similarity Surface (MESS) analysis (Elith et al. 2011; Fischer et al. 2011). The MESS analysis estimates the similarity between environments used to train the model and the new projected areas for every grid cell (Elith et al. 2011). The analysis was used to detect regions with environments that are outside the range of environments in the training area (Fischer et al. 2011). Climatic similarities between regions and periods were determined by MESS values. Negative values represent non-analogue climatic conditions.

Phylogenetic and genetic diversity analysis

A total of 32 individual samples of *S. acupunctatus* were collected in Europe and preserved in 95% ethanol at -20 °C, before genetic analyses. Four other sequences from Liguria (surrounding of Pallanca and Hanbury Botanical Gardens, located in Bordighera and Ventimiglia, respectively, Imperia Province, NW Italy) were already available in CNR-IRET and CREA-DC unpublished collections (Table 1).

Genomic DNA from all samples was extracted using QIAGEN Blood and Tissue kit (Qiagen Inc., USA), following the manufacturer's protocol. A fragment of the mitochondrial DNA Cytochrome Oxidase I (COXI) was amplified and compared with sequences deposited in the GenBank. COXI was amplified using the primers LCO1490: 5'-GGTCAACAAATCATAAAGATATTGG-3' and HCO2198: '5-TAAACTTCAGGGTGACCAAAAAATCA-3' (Folmer et al. 1994). These primers were previously used to amplify the same gene in *S. acupunctatus* from Central America for species-identification purposes (Azuara-Domínguez et al. 2013; Chamorro et al. 2016: Table 2) using the amplification protocol reported by Baratti et al. (2005) and Chamorro et al. (2016).

PCR products were run on a 1.5% agarose gel, then purified (ExoSAP-IT, Amersham Biosciences) and finally sent to BMR Genomics (Padua, Italy) for Sanger sequencing. Electropherograms were visualised with the software Chromas 1.45 (http://www.technelysium.com.au. Accessed on 17.12.2022). The sequences were visually corrected and aligned using ClustalX 2.1 (Thompson et al. 1997), together with all the available COXI sequences of *S. acupunctatus* retrieved from GenBank and BOLD System, for a total of 65 sequences (627–903 bp: Table 2).

The phylogenetic reconstruction was conducted by applying Neighbour Joining (NJ), Bayesian Inference (BI) and Maximum Likelihood (ML) methods.

Table 1. Location of the 32 sampling sites for *Scyphophorus acupunctatus* in Europe. Coordinates are expressed in UTM WGS84.

Sample ID	Location of origin	Country	Latitude (°N) / Longitude (°E)
S1	Isola Rossa - Costa Paradiso, Sardinia	Italy	41.04893°N, 8.93734°E
S2	Isola Rossa - Costa Paradiso, Sardinia	Italy	41.04588°N, 8.93496°E
S3	Isola Rossa - Costa Paradiso, Sardinia	Italy	41.04454°N, 8.93399°E
S4	Isola Rossa - Costa Paradiso, Sardinia	Italy	41.04150°N, 8.92494°E
S5	Isola Rossa - Costa Paradiso, Sardinia	Italy	41.03500°N, 8.92161°E
S6	Isola Rossa - Costa Paradiso, Sardinia	Italy	41.03612°N, 8.92197°E
S7	Isola Rossa - Costa Paradiso, Sardinia	Italy	41.03348°N, 8.91776°E
S8	Isola Rossa - Costa Paradiso, Sardinia	Italy	41.02657°N, 8.89292°E
S9	Isola Rossa - Costa Paradiso, Sardinia	Italy	41.02547°N, 8.89186°E
S10	Isola Rossa - Costa Paradiso, Sardinia	Italy	41.02617°N, 8.89052°E
S22	Villamaniscicle coll del Quirc, Girona	Spain	42.38092°N, 3.07618°E
S23	Villamaniscicle coll del Quirc, Girona	Spain	42.38092°N, 3.07618°E
S29	Tamaracciu, Corsica	France	41.55294°N, 9.31810°E
S30	Isola Rossa - Costa Paradiso, Sardinia	Italy	41.02632°N, 8.88836°E
S31	Isola Rossa - Costa Paradiso, Sardinia	Italy	41.02580°N, 8.88484°E
S32	Isola Rossa - Costa Paradiso, Sardinia	Italy	41.02669°N, 8.88217°E
S33	Isola Rossa - Costa Paradiso, Sardinia	Italy	41.02668°N, 8.88250°E
S34	Isola Rossa - Costa Paradiso, Sardinia	Italy	41.01517°N, 8.88777°E
S35	Isola Rossa - Costa Paradiso, Sardinia	Italy	41.01586°N, 8.88914°E
S36	Isola Rossa - Costa Paradiso, Sardinia	Italy	41.01103°N, 8.88029°E
S37	Isola Rossa - Costa Paradiso, Sardinia	Italy	41.01449°N, 8.87612°E
S38	Isola Rossa - Costa Paradiso, Sardinia	Italy	41.05372°N, 8.94518°E
S44	La Crau, Var	France	43.16317°N, 6.09292°E
S47	Sperlonga, Latium	Italy	41.25847°N, 13.43976°E
S57	Cittadella Universitaria, Catania, Sicily	Italy	37.52546°N, 15.07199°E
S59	Cittadella Universitaria, Catania, Sicily	Italy	37.52546°N, 15.07199°E
S61	Località Balzi Rossi, Ventimiglia, Liguria	Italy	43.78361°N, 7.53638°E
Spal1	Pallanca Garden, Bordighera, Liguria	Italy	43.78835°N, 7.68749°E
Spal2	Pallanca Garden, Bordighera, Liguria	Italy	43.78839°N, 7.68736°E
Shan1	Hanbury Garden, Ventimiglia, Liguria	Italy	43.78408°N, 7.55429°E
Shan2	Hanbury Garden, Ventimiglia, Liguria	Italy	43.78445°N, 7.55415°E
Españ1	Passeig Maritim de la Barceloneta, Barcelona	Spain	41.38474°N, 2.19592°E

The Kimura-2-parameters nucleotide substitution model was selected by jModelTest 2 (Darriba et al. 2012) with the Akaike Information Criterion (AIC) and corrected for rate heterogeneity amongst sites with a Gamma distribution. The NJ was performed by MEGA 11 software with 10,000 bootstrap replicates (Tamura et al. 2021). The BI analysis was performed with MrBayes v.3.12 (Ronquist and Huelsenbeck 2003), using the best model selected. Four chains of Markov Chain Monte Carlo were simultaneously run and sampled every 1000 generations for 4 million generations. The first 1000 sampled trees from each run were discarded as burn-in. The ML phylogenetic analysis was conducted with SeaView software (Gouy et al. 2010). Outgroups (*Dryophthorus corticalis* (Paykull), Stromboscerini sp. and *Aclees taiwanensis* Kôno) were selected in line with their close phylogenetic placement within the family to the study taxon. Nucleotide diversity, haplotype diversity, number of parsimony-informative and variable sites were

Table 2. Accession numbers of sequences used for the phylogenetic reconstructions of *Scyphophorus acupunctatus*.

Accession number	Sampling location	Sampling country	Population status	Reference
AY131110	Not available	Continental USA	Native	Direct submission to GenBank
AY131122	Massachusetts	Continental USA	Native	Direct submission to GenBank
GBCL49633-19	California	Continental USA	Native	Direct submission to BOLD Systems
HM433616	Colorado	Continental USA	Native	Direct submission to GenBank
KU896920	Arizona	Continental USA	Native	Chamorro et al. (2016)
KU896921	Arizona	Continental USA	Native	Chamorro et al. (2016)
KU896922	Arizona	Continental USA	Native	Chamorro et al. (2016)
KU896923	Arizona	Continental USA	Native	Chamorro et al. (2016)
KU896924	Arizona	Continental USA	Native	Chamorro et al. (2016)
JX134898	Not available	Mexico	Native	Azuara-Dominguez et al. (2013)
JX134899	Not available	Mexico	Native	Azuara-Dominguez et al. (2013)
JX134900	Not available	Mexico	Native	Azuara-Dominguez et al. (2013)
JX134901	Not available	Mexico	Native	Azuara-Dominguez et al. (2013)
JX134902	Not available	Mexico	Native	Azuara-Dominguez et al. (2013)
JX134903	Not available	Mexico	Native	Azuara-Dominguez et al. (2013)
JX134904	Not available	Mexico	Native	Azuara-Dominguez et al. (2013)
JX134905	Not available	Mexico	Native	Azuara-Dominguez et al. (2013)
JX134906	Not available	Mexico	Native	Azuara-Dominguez et al. (2013)
JX134907	Not available	Mexico	Native	Azuara-Dominguez et al. (2013)
JX134908	Not available	Mexico	Native	Azuara-Dominguez et al. (2013)
JX134909	Not available	Mexico	Native	Azuara-Dominguez et al. (2013)
JX134910	Not available	Mexico	Native	Azuara-Dominguez et al. (2013)
ASSCR6360-12	Not available	Costa Rica	Most likely native	Direct submission to BOLD Systems
ASSCR6362-12	Not available	Costa Rica	Most likely native	Direct submission to BOLD Systems
KU896927	Not available	Guatemala	Most likely native	Chamorro et al. (2016)
KU896929	Not available	Guatemala	Most likely native	Chamorro et al. (2016)
OQ198464	La Crau	Continental France	Non-native	Present work
OQ198455	Corsica	France	Non-native	Present work
OQ193159	Isola Rossa – Costa Paradiso, Sardinia	Italy	Non-native	Present work
OQ193160	Isola Rossa – Costa Paradiso, Sardinia	Italy	Non-native	Present work
OQ193161	Isola Rossa – Costa Paradiso, Sardinia	Italy	Non-native	Present work
OQ193162	Isola Rossa – Costa Paradiso, Sardinia	Italy	Non-native	Present work
OQ193165	Isola Rossa – Costa Paradiso, Sardinia	Italy	Non-native	Present work
OQ193176	Isola Rossa – Costa Paradiso, Sardinia	Italy	Non-native	Present work
OQ193177	Isola Rossa – Costa Paradiso, Sardinia	Italy	Non-native	Present work
OQ194007	Isola Rossa – Costa Paradiso, Sardinia	Italy	Non-native	Present work
OQ194008	Isola Rossa – Costa Paradiso, Sardinia	Italy	Non-native	Present work

Accession number	Sampling location	Sampling country	Population status	Reference
OQ194015	Isola Rossa – Costa Paradiso, Sardinia	Italy	Non-native	Present work
OQ194016	Isola Rossa – Costa Paradiso, Sardinia	Italy	Non-native	Present work
OQ198466	Isola Rossa – Costa Paradiso, Sardinia	Italy	Non-native	Present work
OQ194025	Isola Rossa – Costa Paradiso, Sardinia	Italy	Non-native	Present work
OQ194031	Isola Rossa – Costa Paradiso, Sardinia	Italy	Non-native	Present work
OQ194033	Isola Rossa – Costa Paradiso, Sardinia	Italy	Non-native	Present work
OQ198456	Isola Rossa – Costa Paradiso, Sardinia	Italy	Non-native	Present work
OQ198458	Isola Rossa – Costa Paradiso, Sardinia	Italy	Non-native	Present work
OQ198459	Isola Rossa – Costa Paradiso, Sardinia	Italy	Non-native	Present work
OQ198460	Isola Rossa – Costa Paradiso, Sardinia	Italy	Non-native	Present work
OQ194017	Balzi Rossi, Ventimiglia, Liguria	Italy	Non-native	Present work
OQ198461	Pallanca Gardens, Liguria	Italy	Non-native	Present work
OQ198457	Pallanca Gardens, Liguria	Italy	Non-native	Present work
OQ193174	Hanbury Gardens, Liguria	Italy	Non-native	Present work
OQ198462	Hanbury Gardens, Liguria	Italy	Non-native	Present work
OQ194018	Catania, Sicily	Italy	Non-native	Present work
OQ194019	Catania, Sicily	Italy	Non-native	Present work
OQ198463	Sperlonga, Latium	Italy	Non-native	Present work
OQ193157	Villamaniscicle	Spain	Non-native	Present work
OQ193158	Villamaniscicle	Spain	Non-native	Present work
OQ193175	Passeig Maritim de la Barceloneta, Barcelona	Spain	Non-native	Present work
MW520550	Porto Santo	Portugal	Non-native	Stüben et al. (2021)
HM433615	Not available	Virgin Islands	Non-native	Direct submission to GenBank
KU896925	Not available	Virgin Islands	Non-native	Chamorro et al. (2016)
KU896926	Not available	Virgin Islands	Non-native	Chamorro et al. (2016)
KU896928	Not available	Virgin Islands	Non-native	Chamorro et al. (2016)
KU896931	Not available	Virgin Islands	Non-native	Chamorro et al. (2016)
KU896932	Not available	Virgin Islands	Non-native	Chamorro et al. (2016)

computed both for the native and the invaded ranges of *S. acupunctatus* through Mega XI (Tamura et al. 2021). A Templeton, Crandall and Sing (TCS) parsimony Network (Clement et al. 2000) connecting haplotypes was obtained with popART (http://popart.otago.ac.nz, Accessed on 20.12.2022) with the aim to visualise the relationship amongst the new and previously-described mitochondrial haplotypes (see Sciandra et al. (2022)).

Results

Species distribution

Overall, the agave weevil was reported on all continents, except for Antarctica. Based on genetic analyses and literature, the native range of this species includes the USA, Mexico and, most likely, the rest of continental Central America (Vaurie 1971). The invasive range of this species (Fig. 1a) includes four South American countries (Brazil, Colombia, Ecuador and Venezuela), the insular USA (including Hawaii and Virgin Islands), Caribbean islands, southern European countries (Portugal including Madeira, Spain including Canary and Balearic Islands, Italy including Sardinia, Sicily and several small islands, Greece including Aegean Islands, Croatian islands and Cyprus), South Africa, Kenya, Tanzania, Saudi Arabia, Java, Sumatra, Borneo and southern Australia (Fig. 1b). Occurrences from other countries (i.e. Israel, the Netherlands, UK and Argentina) were not confirmed and may represent single interceptions.

Species distribution models

Projections of each statistical model (Suppl. material 1: fig. S5) produced slightly different results that were averaged in the ensemble model. The ensemble model for current climate showed a high climatic suitability in the native range and in some parts of the non-native range, i.e. the eastern areas of South Africa, the northern Rift Valley (i.e. from Eritrea and Ethiopia to Tanzania), parts of South America and the central and western Mediterranean countries (Fig. 2a). Highly suitable areas were also predicted in southern Australia, where *S. acupunctatus* has been scarcely recorded so far, the area around the Caspian Sea and the Middle East, where the weevil has not yet been recorded (Fig. 2a).

Considering future climate scenarios forecast for 2070, the areas suitable for *S. acupunctatus* would increase especially towards temperate-cold latitudes, both in Europe and worldwide (Fig. 2b).

Values representing the degree of climatic similarity between future and present conditions are shown in Fig. 2c, with an increase in suitability of 72.62% and a decrease of 27.43%, based on the number of cells around the Globe. There was agreement between the different algorithms used to predict the species' distribution under future climates (Fig. 2d; Suppl. material 1: fig. S5). The climate suitability of most temperate areas of both Hemispheres will increase for *S. acupunctatus* in the future.

The MESS analysis showed that the projection area shared a medium to high environmental similarity with many countries in the training area, except for a few northern Eurasian areas (Suppl. material 1: fig. S6).

Genetic analyses

The COXI sequences were obtained from all analysed samples. All sequences generated in the present study were deposited in GenBank (Table 2). The alignment of COXI gene

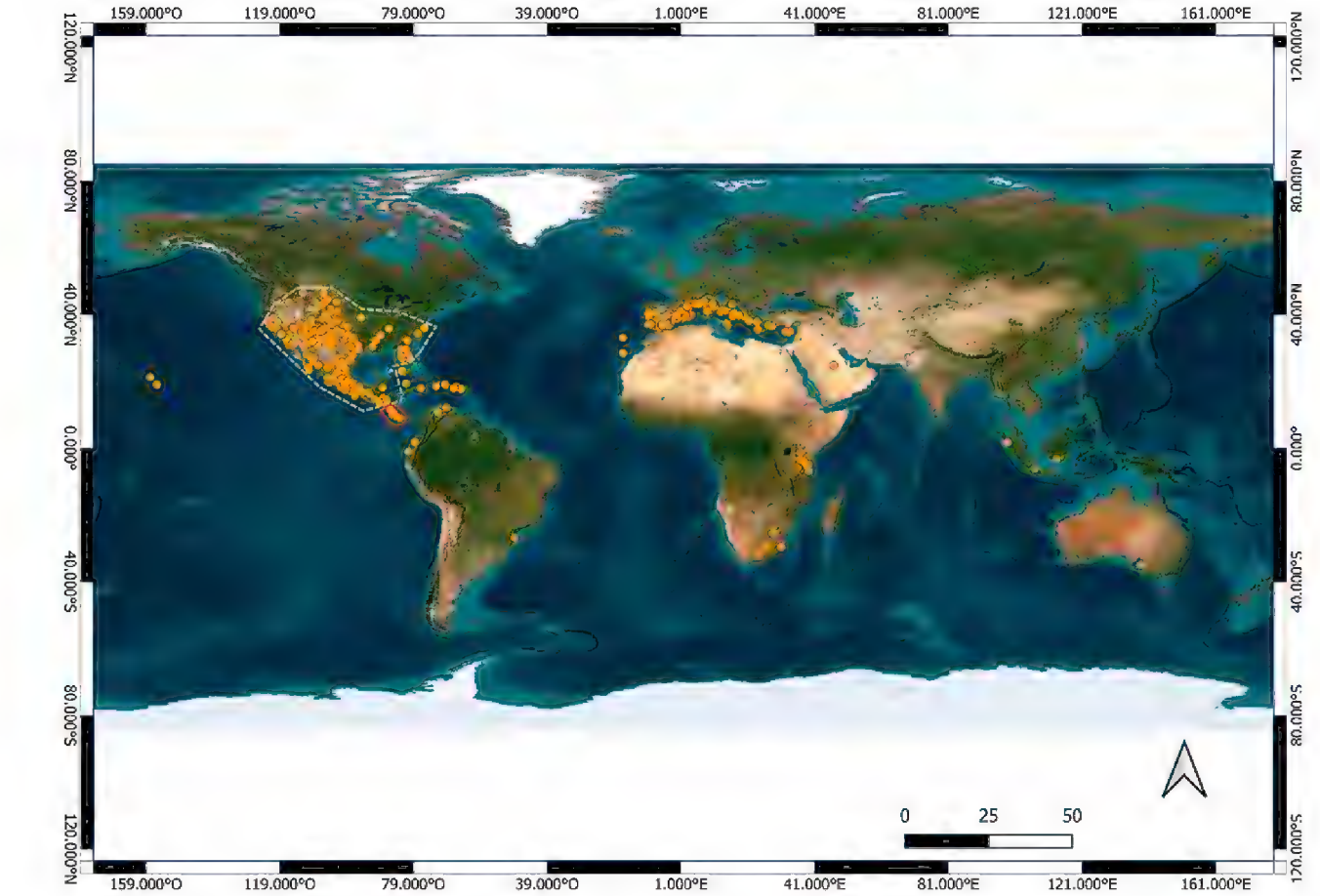

Figure 1. a Worldwide distribution of *Scyphophorus acupunctatus* in both native (central and southern North America) and non-native ranges (n = 1135 occurrences) **b** distribution of *S. acupunctatus* in southern European Countries (orange dots refer to occurrence sites of agave weevil). The white dotted line includes occurrences from the native range, whereas the solid red line includes occurrences of uncertain origin. Occurrences outside dotted lines are non-native populations. Sources: Data SIO, NOAA, US Navy, NGA, GEBCO 2016 TerraMetrics 2016 Google; Wikimedia Commons, user Norman Einstein, CC-BY-SA-3.0.

consists of 627–903 nucleotides for 65 individuals, including 32 from the Mediterranean area. All individuals belonged to *S. acupunctatus*, as no record of *S. yuccae* was confirmed in the analysed samples nor in any sequence deposited in the GenBank. Nucleotide and haplotype diversity was lower in the alien than in the non-native range (Table 3).

An ML tree is presented in Fig. 3 and supports the monophyly of *S. acupunctatus* (Fig. 3). Samples from the native range (Mexico and Continental USA) clustered to-

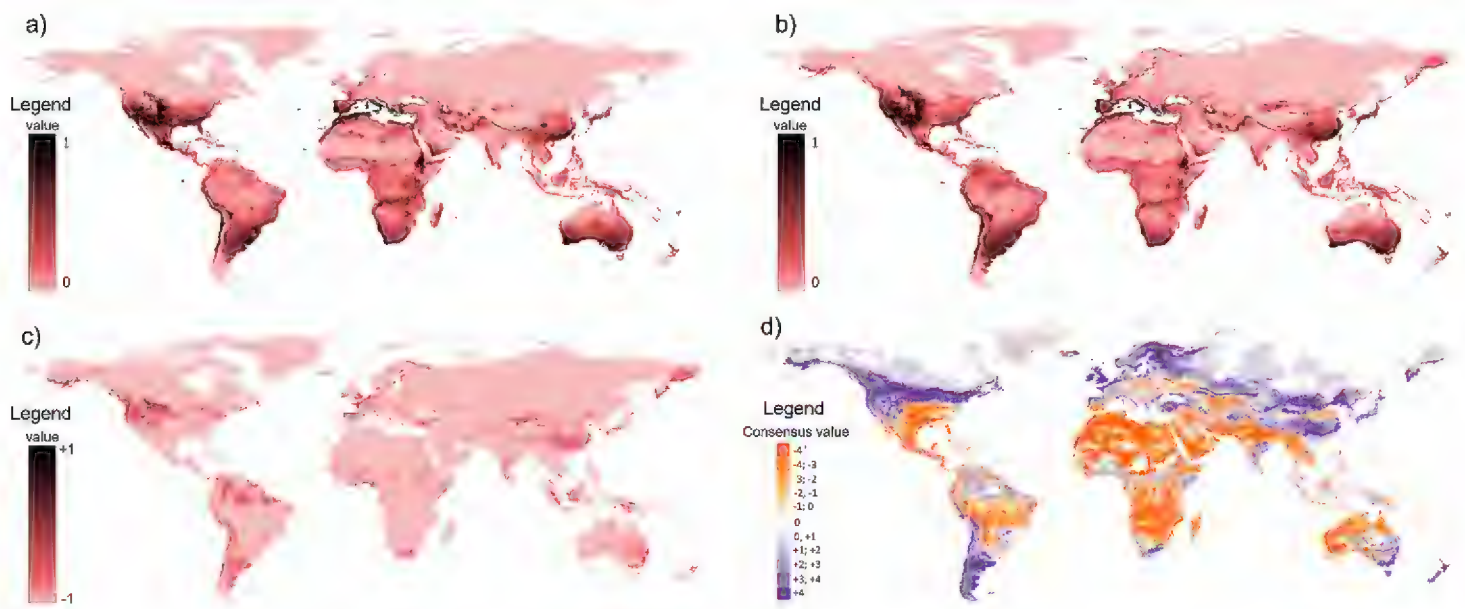

Figure 2. a Current potential distribution of *Scyphophorus acupunctatus* worldwide (suitability increasing from pink to black) **b** future potential distribution of *S. acupunctatus* under climate projections using the global climate model for 2070 (suitability increasing from pink to black) **c** differences between future and present conditions [future-current] for the RCP 2.6 scenario obtained by subtracting, for each cell, the predicted suitability under current climate from that under future climates. Pink to black: increase in climatic suitability in the future **d** consensus change for RCP 2.6 scenario. Dark blue (+4) indicates that all models predicted an increase in suitability, whereas dark orange (-4) indicates a full agreement in predicting a decrease in suitability; white indicates disagreement across models (0 value).

Table 3. Indices of genetic diversity for native and most-likely native (n = 26 samples) and non-native (n = 39 samples) populations of *Scyphophorus acupunctatus* (cf. Table 2).

	Total	**Native and most-likely native populations**	**Alien populations**
π (nucleotide diversity index ± standard deviation)	0.22 ± 0.05	0.59 ± 0.05	0.03 ± 0.01
h (haplotype diversity index ± standard deviation)	0.42 ± 0.15	0.61 ± 0.19	0.09 ± 0.01
Number of segregating sites	170	161	115
Number of Parsimony Informative sites	154	148	71

gether and represented the sister group of the clade that included samples from southern countries of Central America (Costa Rica and Guatemala) and all the non-native range (Fig. 3).

The TCS network highlighted that the majority of introduced individuals in Sardinia, Sicily, Corsica, continental Italy (Latium and Liguria), continental France, Spain and Portugal belonged to the same haplotype, as in Costa Rica and Guatemala (Fig. 4).

Discussion

This study showed for the first time the actual and potential global distribution of the agave weevil, both in the native and non-native ranges and assessed the phylogenetic relationships between native and non-native populations at the global scale.

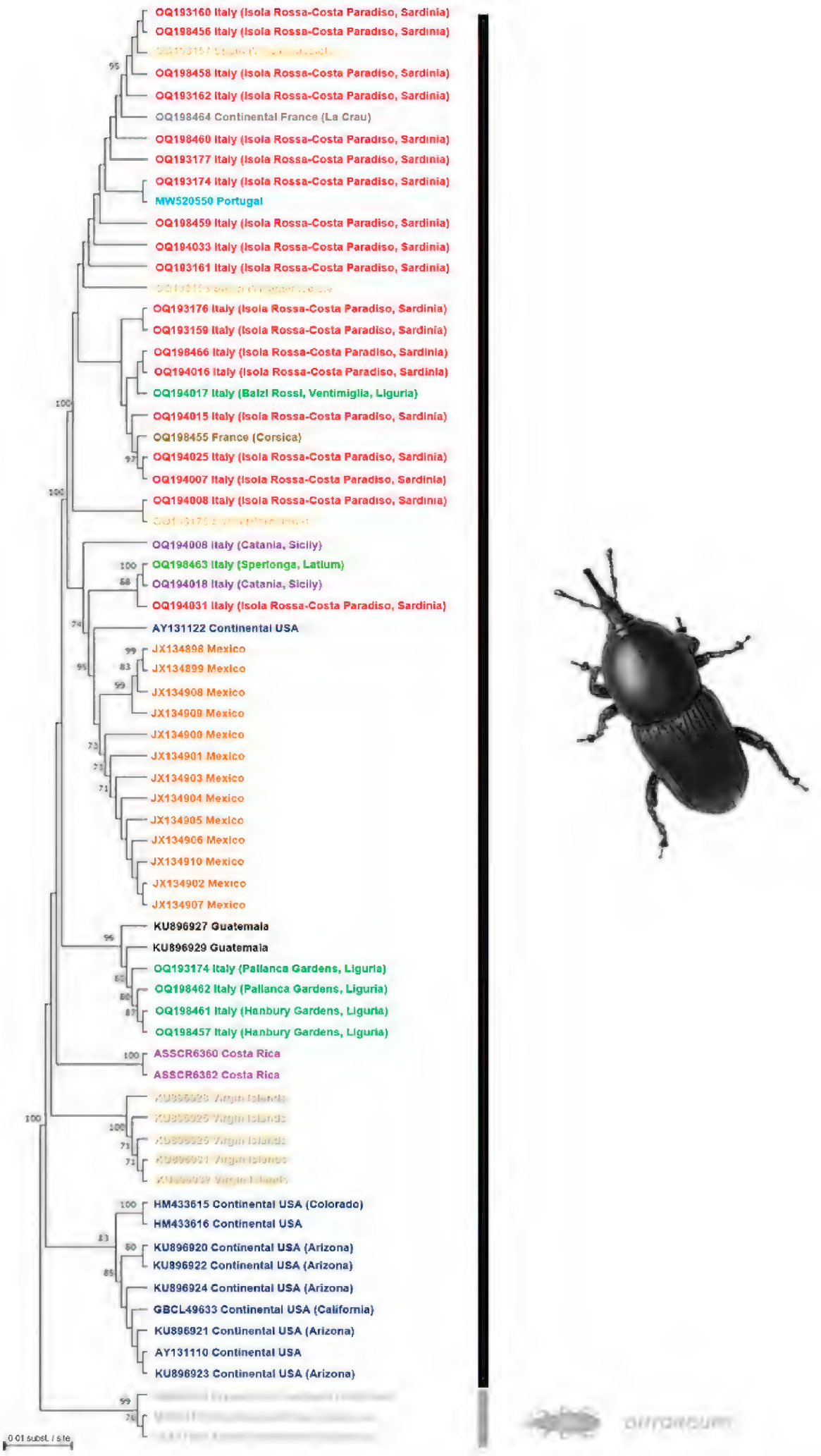

Figure 3. Maximum Likelihood (ML) phylogenetic tree obtained from the analysis of COXI for 65 individuals of *Scyphophorus acupunctatus* (n = 39 from non-native range, n = 22 from native range, n = 4 from most-likely native range, cf. Table 2). The statistical support of major clades is shown at their nodes (NJ Bootstrap support/Bayesian probabilities/ML Bootstrap support).

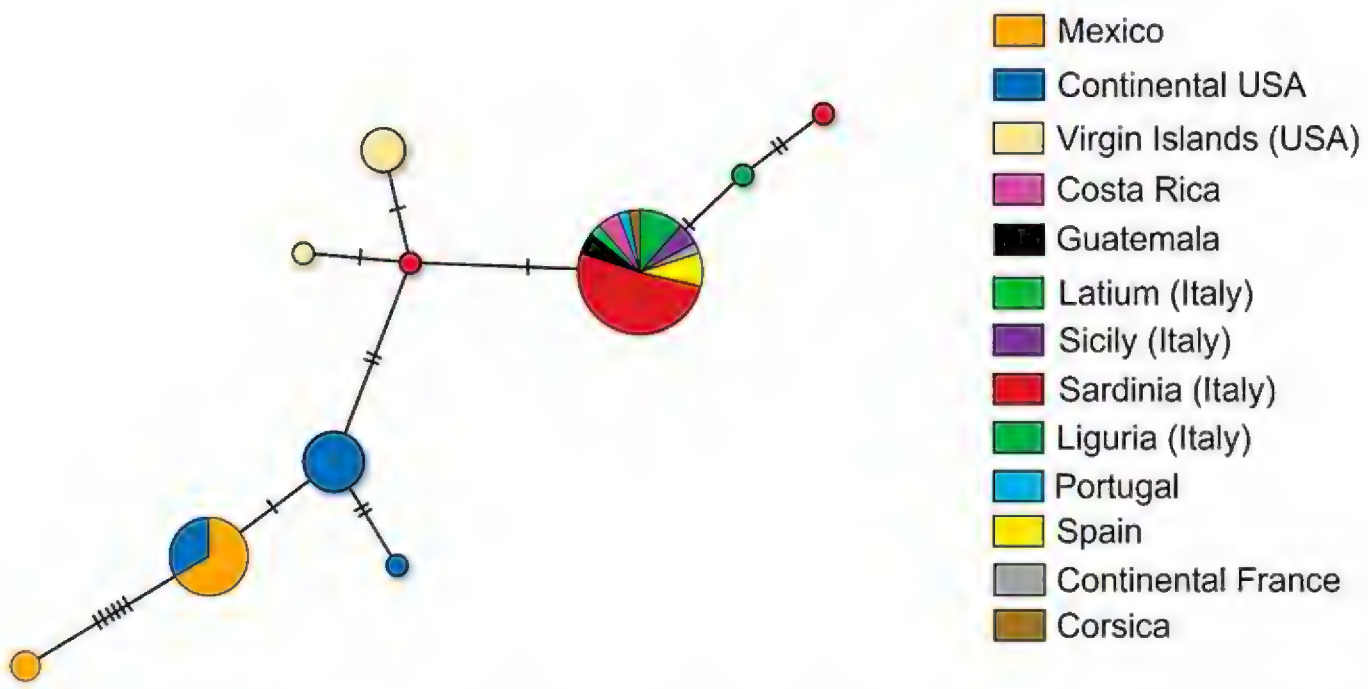

Figure 4. *Scyphophorus acupunctatus* TCS Network showing the relationship amongst mitochondrial COXI haplotypes. Circles represent different haplotypes (n = 10). Circle size is proportional to the number of samples for each haplotype. Mutations are shown as hatch marks.

The presence of this species was confirmed in several countries, whereas some of those listed in CABI's overview of invasive species (the Netherlands, UK, Israel, New Zealand and Argentina: CABI (2023)) were not confirmed. In contrast, the occurrence of non-native *S. acupunctatus* was reported for the first time in Ecuador, through the iNaturalist repository, as well as in many Italian regions where this weevil was previously not reported (Calabria, Sardinia, Piedmont and Campania: Suppl. material 1: fig. S7). In particular, the first record of this weevil in Sardinia, in the north-western part of the island, was due to detailed and addressed research by the authors of this work.

Despite being reported as the most important pest for agave species (Waring and Smith 1986), the agave weevil is not commonly identified by the public; thus, it is unsuitable for citizen-science surveys (cf. Mazza et al. (2020) for *C. ayyari*). Accordingly, most data on the distribution of this species were obtained from scientific research and insect monitoring projects conducted by specialists (Kontodimas and Kallinikou 2010; Vassiliou and Kitsis 2015). The occurrence of the agave weevil was also confirmed in all the other regions where it was previously reported, i.e. Sicily, Basilicata, Apulia, Latium, Tuscany and Liguria, as well as some small Thyrrenian islands (i.e. Giglio, Elba, Giannutri and Ponza).

The presence of the agave weevil in other Italian peninsular regions along the coastline (e.g. Molise, Abruzzo, Marche, Emilia Romagna and Veneto) cannot be ruled out. Thus, a focused monitoring programme is required, particularly in late spring and during the daytime, when most observations occur (López-Martínez et al. 2011; Figueroa Castro et al. 2013).

Species distribution modelling showed a high climatic suitability for this species throughout the Mediterranean Basin, potentially increasing with increasing temperature and decreasing precipitation, i.e. with the ongoing climatic change. Accordingly, the native range of *S. acupunctatus* currently includes mostly dry areas of Central

America, also suggesting the adaptation of this insect to hot desert areas (including mountainous ones), where most Agavaceae, i.e. succulent plants representing the staple of its diet and reproductive sites, grow. The distribution of *S. acupunctatus* in Europe and Africa is linked to the distribution of Agavaceae and Dracaenaceae as ornamental plants. Particularly, in the Mediterranean countries, these plants mostly occur in botanical gardens and along the coastline, i.e. where most records of *S. acupunctatus* have been reported (Smith and Figueiredo 2007; Celesti Grapow et al. 2016; Cascone et al. 2021).

Genetic analyses showed a strong genetic uniformity for the non-native populations. A lower nucleotide and haplotype diversity was observed in the non-native range compared to the native range, possibly due to a founder effect. The presence of a single widespread haplotype in Europe suggested that most of the introductions may have originated from a small geographical area in Central America or a small number of introduction events occurred. This contrasts with other species, which were introduced through multiple unintentional introductions in Europe. These include *C. ayyari*, *H. halys* and *Megachile* (*Callomegachile*) *sculpturalis* Smith, which show a high genetic diversity linked to several introduction events (Cesari et al. 2018; Mazza et al. 2020; Lanner et al. 2021). *Scyphophorus acupunctatus* in Europe may have originated from one or a few introduction events from Central America (most likely from Guatemala or Costa Rica) through the ornamental plant trade (Global Invasive Species Database 2023). This is in line with EPPO's report (EPPO 2022b), which traces the source of the first introduction of agave weevil to Italy to countries of southern Central America, based on interception data.

Driving definite conclusions from single-gene analyses may be misleading. However, the largest genetic library for *S. acupunctatus* built in the present study may serve as a comparison for future studies and for species identification (Azuara-Domínguez et al. 2013; Chamorro et al. 2016). All analysed samples belonged to *S. acupunctatus* and the only deposited sequence of the sister species *S. yuccae* on GenBank suggests that this species could be a synonym to *S. acupunctatus*, as already hypothesised by Chamorro et al. (2016).

In general, our data showed a high climatic suitability for *S. acupunctatus* in Eurasia and Africa (particularly in the Mediterranean Basin coastline), including areas where this weevil is not yet present. This suggests that if no management actions are taken to limit its spread, there is potential for range expansion towards continental and temperate Europe in the upcoming years. Given the impacts on cultivated agave plants, early detection of this species in new areas should be promoted to prevent further invasions, by means of free online citizen-science platforms and coordination of phytosanitary services and national institutions for the prevention of biological invasions.

Acknowledgements

This work was supported by CNR: Research project FOE – Capitale Naturale e Risorse per il Futuro dell'Italia and Progetto di Ricerca@CNR – USEit Utilizzo di sinergie operative per lo studio e la gestione integrata di specie aliene invasive in Italia.

AC gratefully acknowledges Project ALIEM APOSTROPHE "Action pour Limiter les risques de diffusion des espèces Introduites Envahissantes en Méditerranée" PC IFM 2014–2020 for financial support. Authors would like to thank E. Colonnelli, M. Depratis, L. Forbicioni, E. Giroux, S. Longo, L. Nuccitelli, E. Vandel, C. Berquier and J. Ventura who collected, provided or identified samples of *Scyphophorus acupunctatus*. We wish also to thank G. Mazza and E. Mori who provided us with four unpublished genetic sequences from Liguria. Moreover, we also thank M. Baratti and E. Paoletti, who allowed us to conduct genetic analyses at the CNR-IRET laboratories in Sesto Fiorentino. The Italian Legislative Decree 19/2021 ("Rules for the protection of plants from harmful organisms") imposes that any previously unrecorded species in any Italian region must be immediately reported to the National Phytosanitary Service before any publication (both scientific and newspaper articles). Therefore, updated information on the distribution of this species in Italy has been sent to all Directors of Regional Phytosanitary Service before this publication. We are indebted with L. Pasquali, L. Ancillotto, M. Di Febbraro, L. Bosso, M. Falaschi and D. Strubbe, who provided us with deep help in species distribution model analyses. To conclude, we would like to thank the Subject Editor, Dr. Katelyn Faulkner and two reviewers for the insightful comments they provided on our early manuscript.

References

Aiello-Lammens ME, Boria RA, Radosavljevic A, Vilela B, Anderson RP (2015) spThin: An R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography 38(5): 541–545. https://doi.org/10.1111/ecog.01132

Alin A (2010) Multicollinearity. Wiley Interdisciplinary Reviews: Computational Statistics 2(3): 370–374. https://doi.org/10.1002/wics.84

Ancillotto L, Strubbe D, Menchetti M, Mori E (2016) An overlooked invader? Ecological niche, invasion success and range dynamics of the Alexandrine parakeet in the invaded range. Biological Invasions 18(2): 583–595. https://doi.org/10.1007/s10530-015-1032-y

Ancillotto L, Bosso L, Smeraldo S, Mori E, Mazza G, Herkt M, Galimberti A, Ramazzotti F, Russo D (2020) An African bat in Europe, *Plecotus gaisleri*: Biogeographic and ecological insights from molecular taxonomy and Species Distribution Models. Ecology and Evolution 10(12): 5785–5800. https://doi.org/10.1002/ece3.6317

Ancillotto L, Viviano A, Baratti M, Sogliani D, Ladurner E, Mori E (2023) Every branch in its niche: Intraspecific variation in habitat suitability of a widely distributed small mammal, the harvest mouse *Micromys minutus*. Mammal Research 68(4): 575–585. https://doi.org/10.1007/s13364-023-00693-3

Andrade MM (2022) The presence of the Agave weevil *Scyphophorus acupunctatus* Gyllenhal, 1838 (Coleoptera: Dryophthoridae) in Madeira Archipelago. A new biological control opportunity or a new invasive species? Weevil News 98: 1–2.

Aquino-Bolaños T, Ortiz-Hernández YD, Martiínez-Gutiérrez GA (2013) Relationship between *Scyphophorus acupunctatus* Gyllenhal damage and nutrient and sugar content of

Agave angustifolia Haw. The Southwestern Entomologist 38(3): 477–486. https://doi.org/10.3958/059.038.0310

Araújo MB, New M (2007) Ensemble forecasting of species distributions. Trends in Ecology & Evolution 22(1): 42–47. https://doi.org/10.1016/j.tree.2006.09.010

Atauchi PJ, Peterson AT, Flanagan J (2018) Species distribution models for Peruvian plantcutter improve with consideration of biotic interactions. Journal of Avian Biology 49(3): jav-01617. https://doi.org/10.1111/jav.01617

Azuara-Domínguez A, Cibrián-Tovar J, Terán-Vargas AP, Segura-León OL, Cibrián-Jaramillo A (2013) Factors in the response of Agave Weevil, *Scyphophorus acupunctatus* (Coleoptera: Curculionidae), to the major compound in its aggregation pheromone. The Southwestern Entomologist 38(2): 209–220. https://doi.org/10.3958/059.038.0206

Banks NC, Paini DR, Bayliss KL, Hodda M (2015) The role of global trade and transport network topology in the human-mediated dispersal of alien species. Ecology Letters 18(2): 188–199. https://doi.org/10.1111/ele.12397

Baratti M, Goti E, Messana G (2005) High level of genetic differentiation in the marine isopod *Sphaeroma terebrans* (Crustacea Isopoda Sphaeromatidae) as inferred by mitochondrial DNA analysis. Journal of Experimental Marine Biology and Ecology 315(2): 225–234. https://doi.org/10.1016/j.jembe.2004.09.020

Barber RA, Ball SG, Morris RK, Gilbert F (2022) Target-group backgrounds prove effective at correcting sampling bias in Maxent models. Diversity & Distributions 28(1): 128–141. https://doi.org/10.1111/ddi.13442

Biondi A, Guedes RNC, Wan FH, Desneux N (2018) Ecology, worldwide spread, and management of the invasive South American tomato pinworm, *Tuta absoluta*: Past, present, and future. Annual Review of Entomology 63(1): 239–258. https://doi.org/10.1146/annurev-ento-031616-034933

Bolaños TA, Velázquez EP, Hernández UÁ, Gamboa JRD (2014) Host plants of the agave weevil *Scyphophorus acupunctatus* (Gyllenhal) (Coleoptera: Curculionidae) in Oaxaca, Mexico. The Southwestern Entomologist 39(1): 163–169. https://doi.org/10.3958/059.039.0115

Buisson L, Thuiller W, Casajus N, Lek S, Grenouillet G (2010) Uncertainty in ensemble forecasting of species distribution. Global Change Biology 16(4): 1145–1157. https://doi.org/10.1111/j.1365-2486.2009.02000.x

Buonincontri MP, Bosso L, Smeraldo S, Chiusano ML, Pasta S, Di Pasquale G (2023) Shedding light on the effects of climate and anthropogenic pressures on the disappearance of *Fagus sylvatica* in the Italian lowlands: Evidence from archaeo-anthracology and spatial analyses. The Science of the Total Environment 877: 162893. https://doi.org/10.1016/j.scitotenv.2023.162893

CABI (2023) *Scyphophorus acupunctatus* (agave weevil). https://www.cabidigitallibrary.org/doi/10.1079/cabicompendium.49421 [Accessed on 10.02.2023]

CABI/EPPO (2014) *Scyphophorus acupunctatus* [Distribution map]. Distribution Maps of Plant Pests. CABI, Wallingford, Map 66 (2nd revision). https://doi.org/10.1079/DMPP/20153006587

Cancellario T, Laini A, Wood PJ, Guareschi S (2023) Among demons and killers: Current and future potential distribution of two hyper successful invasive gammarids. Biological Invasions 25(5): 1627–1642. https://doi.org/10.1007/s10530-023-03000-y

Cascone S, Sperandii MG, Cao Pinna L, Marzialetti F, Carranza ML, Acosta ATR (2021) Exploring temporal trends of plant invasion in Mediterranean coastal dunes. Sustainability (Basel) 13(24): 13946. https://doi.org/10.3390/su132413946

CBD [Convention for Natural Biodiversity] (2010) What are Invasive Alien Species? https://www.cbd.int/invasive/WhatareIAS.shtml [Accessed on 09.01.2023]

Celesti-Grapow L, Bassi L, Brundu G, Camarda I, Carli E, D'Auria G, Del Guacchio E, Domina G, Ferretti G, Foggi B, Lazzaro L, Mazzola P, Peccenini S, Pretto F, Stinca A, Blasi C (2016) Plant invasions on small Mediterranean islands: An overview. Plant Biosystems 150(5): 1119–1133. https://doi.org/10.1080/11263504.2016.1218974

Cesari M, Maistrello L, Piemontese L, Bonini R, Dioli P, Lee W, Chang-Gyu P, Partsinevelos GK, Rebecchi L, Guidetti R (2018) Genetic diversity of the brown marmorated stink bug *Halyomorpha halys* in the invaded territories of Europe and its patterns of diffusion in Italy. Biological Invasions 20(4): 1073–1092. https://doi.org/10.1007/s10530-017-1611-1

Chamberlain S, Ram K, Hart T (2017) Spocc: interface to species occurrence data sources (version 0.7.0). https://cran.r-project.org/web/packages/spocc/index.html [Accessed on 10.05.2023]

Chamorro ML, Persson J, Torres-Santana CW, Keularts J, Scheffer SJ, Lewis ML (2016) Molecular and morphological tools to distinguish *Scyphophorus acupunctatus* Gyllenhal, 1838 (Curculionidae: Dryophthorinae): a new weevil pest of the endangered century plant, *Agave eggersiana* from St. Croix, US Virgin Islands. Proceedings of the Entomological Society of Washington 118(2): 218–243. https://doi.org/10.4289/0013-8797.118.2.218

Cianferoni F, Graziani F, Dioli P, Ceccolini F (2018) Review of the occurrence of *Halyomorpha halys* (Hemiptera: Heteroptera: Pentatomidae) in Italy, with an update of its European and World distribution. Biologia 73(6): 599–607. https://doi.org/10.2478/s11756-018-0067-9

Clement M, Posada D, Crandall KA (2000) TCS: A computer program to estimate gene genealogies. Molecular Ecology 9(10): 1657–1660. https://doi.org/10.1046/j.1365-294x.2000.01020.x

Cocco A, Brundu G, Berquier C, Andreï-Ruiz MC, Pusceddu M, Porceddu M, Podda L, Satta A, Petit Y, Floris I (2021) Establishment and new hosts of the non-native seed beetle *Stator limbatus* (Coleoptera, Chrysomelidae, Bruchinae) on acacias in Europe. NeoBiota 70: 167–192. https://doi.org/10.3897/neobiota.70.70441

Colombo M (2000) First record of *Scyphophorus acupunctatus* (Coleoptera Curculionidae) in Italy. Bollettino di Zoologia Agraria e di Bachicoltura 32: 165–170.

Crase B, Liedloff A, Vesk PA, Fukuda Y, Wintle BA (2014) Incorporating spatial autocorrelation into species distribution models alters forecasts of climate-mediated range shifts. Global Change Biology 20(8): 2566–2579. https://doi.org/10.1111/gcb.12598

Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: More models, new heuristics and parallel computing. Nature Methods 9(8): 772. https://doi.org/10.1038/nmeth.2109

De Marco Jr P, Diniz-Filho JAF, Bini LM (2008) Spatial analysis improves species distribution modelling during range expansion. Biology Letters 4(5): 577–580. https://doi.org/10.1098/rsbl.2008.0210

Deutsch CA, Tewksbury JJ, Tigchelaar M, Battisti DS, Merrill SC, Huey RB, Naylor RL (2018) Increase in crop losses to insect pests in a warming climate. Science 361(6405): 916–919. https://doi.org/10.1126/science.aat3466

Di Cola V, Broennimann O, Petitpierre B, Breiner FT, D'Amen M, Randin C, Engler R, Pottier J, Pio D, Dubuis A, Pellissier L, Mateo RG, Hordijk W, Salamin N, Guisan A (2017) ecospat: An R package to support spatial analyses and modeling of species niches and distributions. Ecography 40(6): 774–787. https://doi.org/10.1111/ecog.02671

Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ (2011) A statistical explanation of MaxEnt for ecologists. Diversity & Distributions 17(1): 43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x

EPPO (2008) First record of *Scyphophorus acupunctatus* in France. EPPO Reporting Service 11: 2008/220. https://gd.eppo.int/reporting/article-843 [Accessed on 23.12.2022]

EPPO (2022a) EPPO Global database. EPPO Global database, Paris, France: EPPO, 1 pp. https://gd.eppo.int/ [Accessed on 10.12.2022]

EPPO (2022b) Update on the situation of *Scyphophorus acupunctatus* in Italy. EPPO Reporting Service 7: 2022/149. https://gd.eppo.int/reporting/article-7380 [Accessed on 23.12.2022]

ESRI (2011) ArcGIS Desktop: Release 10. Environmental Systems Research Institute, Redlands, California, USA.

Farina P, Mazza G, Benvenuti C, Cutino I, Giannotti P, Conti B, Bedini G, Gargani E (2020) Biological notes and distribution in Southern Europe of *Aclees taiwanensis* Kôno, 1933 (Coleoptera: Curculionidae): a new pest of the fig tree. Insects 12(1): 5. https://doi.org/10.3390/insects12010005

Fick SE, Hijmans RJ (2017) WorldClim 2: New 1 km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37(12): 4302–4315. https://doi.org/10.1002/joc.5086

Figueroa-Castro P, Solís-Aguilar JF, González-Hernández H, Rubio-Cortés R, Herrera-Navarro EG, Castillo-Márquez LE, Rojas JC (2013) Population dynamics of *Scyphophorus acupunctatus* (Coleoptera: Curculionidae) on blue agave. The Florida Entomologist 96(4): 1454–1462. https://doi.org/10.1653/024.096.0425

Figueroa-Castro P, Rodríguez-Rebollar H, González-Hernández H, Solís-Aguilar JF, del Real-Laborde JI, Carrillo-Sánchez JL, Rojas JC (2016) Attraction range and inter-trap distance of pheromone-baited traps for monitoring *Scyphophorus acupunctatus* (Coleoptera: Dryophthoridae) on blue agave. The Florida Entomologist 99(1): 94–99. https://doi.org/10.1653/024.099.0117

Fischer D, Thomas SM, Niemitz F, Reineking B, Beierkuhnlein C (2011) Projection of climatic suitability for *Aedes albopictus* Skuse (Culicidae) in Europe under climate change conditions. Global and Planetary Change 78(1–2): 54–64. https://doi.org/10.1016/j.gloplacha.2011.05.008

Flinch JM, Alonso-Zarazaga MA (2007) El picudo negro de la pita o agave, o max del henequén, *Scyphophorus acupunctatus* Gyllenhal, 1838 (Coleoptera: Dryophthoridae): primera cita para la Península Ibérica. Boletin de la SEA 41: 419–422.

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3: 294–299.

Foster DR, Motzkin G, Bernardos D, Cardoza J (2002) Wildlife dynamics in the changing New England landscape. Journal of Biogeography 29(10–11): 1337–1357. https://doi.org/10.1046/j.1365-2699.2002.00759.x

Fourcade Y, Engler J, Rödder D, Secondi J (2014) Mapping species distributions with MAXENT using a geographically biased sample of presence data: A performance assessment of methods for correcting sampling bias. PLoS ONE 9(5): e97122. https://doi.org/10.1371/journal.pone.0097122

Geier PW (1966) Management of insect pests. Annual Review of Entomology 11(1): 471–490. https://doi.org/10.1146/annurev.en.11.010166.002351

Global Invasive Species Database (2023) Species profile: *Scyphophorus acupunctatus*. http://www.iucngisd.org/gisd/speciesname/Scyphophorus+acupunctatus [Accessed on 15-01-2023]

Gouy M, Guindon S, Gascuel O (2010) SeaView version 4: A multiplatform graphical user interface for sequence alignment and phylogenetic tree building. Molecular Biology and Evolution 27(2): 221–224. https://doi.org/10.1093/molbev/msp259

Guevara L, Gerstner BE, Kass JM, Anderson RP (2018) Toward ecologically realistic predictions of species distributions: A cross-time example from tropical montane cloud forests. Global Change Biology 24(4): 1511–1522. https://doi.org/10.1111/gcb.13992

Guzmán NV, Lanteri AA, Confalonieri VA (2012) Colonization ability of two invasive weevils with different reproductive modes. Evolutionary Ecology 26(6): 1371–1390. https://doi.org/10.1007/s10682-012-9564-4

Hao T, Elith J, Guillera-Arroita G, Lahoz-Monfort JJ (2019) A review of evidence about use and performance of species distribution modelling ensembles like BIOMOD. Diversity & Distributions 25(5): 1–14. https://doi.org/10.1111/ddi.12892

Horsák M, Limondin-Lozouet N, Juřičková L, Granai S, Horáčková J, Legentil C, Ložek V (2019) Holocene succession patterns of land snails across temperate Europe: East to west variation related to glacial refugia, climate and human impact. Palaeogeography, Palaeoclimatology, Palaeoecology 524: 13–24. https://doi.org/10.1016/j.palaeo.2019.03.028

Huxman TE, Huxman KA, Stamer MR (1997) Dispersal characteristics of the yucca weevil (*Scyphophorus yuccae*) in a flowering field of *Yucca whipplei*. The Great Basin Naturalist 1: 38–43. https://www.jstor.org/stable/41712972

Inghilesi AF, Mazza G, Cervo R, Cini A (2015) A network of sex and competition: The promiscuous mating system of an invasive weevil. Current Zoology 61(1): 85–97. https://doi.org/10.1093/czoolo/61.1.85

Iturbide M, Bedia J, Herrera S, del Hierro O, Pinto M, Gutiérrez JM (2015) A framework for species distribution modelling with improved pseudo-absence generation. Ecological Modelling 312: 166–174. https://doi.org/10.1016/j.ecolmodel.2015.05.018

Kass JM, Muscarella R, Galante PJ, Bohl CL, Pinilla-Buitrago GE, Boria RA, Soley-Guardia M, Anderson RP (2021) ENMeval2.0: Redesigned for customizable and reproducible modeling of species' niches and distributions. Methods in Ecology and Evolution 12(9): 1602–1608. https://doi.org/10.1111/2041-210X.13628

Kock N, Lynn G (2012) Lateral collinearity and misleading results in variance-based SEM: An illustration and recommendations. Journal of the Association for Information Systems 13(7): 1–40. https://doi.org/10.17705/1jais.00302

Kontodimas DC, Kallinikou E (2010) First record of the sisal weevil *Scyphophorus acupunctatus* (Coleoptera: Curculionidae) in Greece. Entomologia Hellenica 19(1): 39–41. https://doi.org/10.12681/eh.11594

Lanner J, Gstöttenmayer F, Curto M, Geslin B, Huchler K, Orr MC, Pachinger B, Sedivy C, Meimberg H (2021) Evidence for multiple introductions of an invasive wild bee species currently under rapid range expansion in Europe. BMC Ecology and Evolution 21(1): 1–15. https://doi.org/10.1186/s12862-020-01729-x

López-Martínez V, Alia-Tejacal I, Andrade-Rodríguez M, De Jesús García-Ramírez M, Rojas JC (2011) Daily activity of *Scyphophorus acupunctatus* (Coleoptera: Curculionidae) monitored with pheromone-baited traps in a field of Mexican tuberose. The Florida Entomologist 94(4): 1091–1093. https://doi.org/10.1653/024.094.0458

Martín-Taboada A, Muñoz AR, Díaz-Ruiz F (2019) Updating the distribution of the exotic agave weevil *Scyphophorus acupunctatus* Gyllenhal, 1838 (Coleoptera: Curculionidae) in peninsular Spain. Anales de Biología 41(41): 49–53. https://doi.org/10.6018/analesbio.41.07

Mattson W, Vanhanen H, Veteli T, Sivonen S, Niemelä P (2007) Few immigrant phytophagous insects on woody plants in Europe: Legacy of the European crucible? Biological Invasions 9(8): 957–974. https://doi.org/10.1007/s10530-007-9096-y

Mazza G, Nerva L, Strangi A, Mori E, Chitarra W, Carapezza A, Mei M, Marianelli L, Roversi PR, Campanaro A, Cianferoni F (2020) Scent of jasmine attracts alien invaders and records on citizen science platforms: multiple introductions of the invasive lacebug *Corythauma ayyari* (Drake, 1933) (Heteroptera: Tingidae) in Italy and the Mediterranean basin. Insects 11(9): 620. https://doi.org/10.3390/insects11090620

Meyerson LA, Mooney HA (2007) Invasive alien species in an era of globalization. Frontiers in Ecology and the Environment 5(4): 199–208. https://doi.org/10.1890/1540-9295(2007)5[199:IASIAE]2.0.CO;2

Montalva J, Sepulveda V, Vivallo F, Silva DP (2017) New records of an invasive bumble bee in northern Chile: Expansion of its range or new introduction events? Journal of Insect Conservation 21(4): 657–666. https://doi.org/10.1007/s10841-017-0008-x

Montoya-Jiménez JC, Valdez-Lazalde JR, Ángeles-Perez G, De Los Santos-Posadas HM, Cruz-Cárdenas G (2022) Predictive capacity of nine algorithms and an ensemble model to determine the geographic distribution of tree species. iForest-Biogeosciences and Forestry 15: 363. https://doi.org/10.3832/ifor4084-015

Mori E, Rustici P, Dapporto L, Pasquali L, Petrucci F, Mazza G (2023) Invasions by the palm borer moth *Paysandisia archon* in Italy and assessment of its trophic spectrum. Biological Invasions 25(5): 1373–1386. https://doi.org/10.1007/s10530-022-02981-6

Mui AB (2015) A multi-temporal remote sensing approach to freshwater turtle conservation. PhD Thesis, University of Toronto, Toronto, 140 pp.

Naimi B, Araújo MB (2016) sdm: A reproducible and extensible R platform for species distribution modelling. Ecography 39(4): 368–375. https://doi.org/10.1111/ecog.01881

Naimi B, Hamm NAS, Groen TA, Skidmore AK, Toxopeus AG (2014) Where is positional uncertainty a problem for species distribution modelling? Ecography 37(2): 191–203. https://doi.org/10.1111/j.1600-0587.2013.00205.x

Palemón-Alberto F, Castañeda-Vildozola Á, Reyes-García G, Domínguez-Monge S, Ramírez YR, Toledo-Hernández E, Toribio-Jiménez J, Terrones-Salgado J, Ortega-Acosta C, Cruz-Lagunas B, Vargas-Ambrosio LF (2022) Damage by *Scyphophorus acupunctatus* Gyllenhal

in Species of Agave. The Southwestern Entomologist 47(2): 437–442. https://doi.org/10.3958/059.047.0219

Parsons SE, Kerner LM, Frank SD (2020) Effects of native and exotic congeners on diversity of invertebrate natural enemies, available spider biomass, and pest control services in residential landscapes. Biodiversity and Conservation 29(4): 1241–1262. https://doi.org/10.1007/s10531-020-01932-8

Pecchi M, Marchi M, Burton V, Giannetti F, Moriondo M, Bernetti I, Bindi M, Chirici G (2019) Species distribution modelling to support forest management. A literature review. Ecological Modelling 411: 108817. https://doi.org/10.1016/j.ecolmodel.2019.108817

Pernek M, Cvetković S (2022) First record of the agave weevil *Scyphophorus acupunctatus* Gyllenhal (Coleoptera, Curculionidae) in Croatia. Entomologia Croatica 21(1): 25–32. https://doi.org/10.17971/ec.21.1.4

Pohjankukka J, Pahikkala T, Nevalainen P, Heikkonen J (2017) Estimating the prediction performance of spatial models via spatial k-fold cross validation. International Journal of Geographical Information Science 31(10): 2001–2019. https://doi.org/10.1080/13658816.2017.1346255

Prakash P (2019) Testing equivalency of interpolation derived bioclimatic variables with actual precipitation: A step towards selecting more realistic explanatory variables for Species Distribution Modelling. Research Journal of Chemistry and Environment 23: 38–41.

QGIS Development Team (2019) QGIS Geographic Information System. Open-Source Geospatial Foundation Project. http://qgis.osgeo.org. [Accessed on 1 April 2023]

R Core Team (2019) R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing. https://www.R-project.org [Accessed on 10.05.2023]

Regos A, Gómez-Rodríguez P, Arenas-Castro S, Tapia L, Vidal M, Domínguez J (2020) Model-assisted bird monitoring based on remotely sensed ecosystem functioning and atlas data. Remote Sensing (Basel) 12(16): 2549. https://doi.org/10.3390/rs12162549

Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics (Oxford, England) 19(12): 1572–1574. https://doi.org/10.1093/bioinformatics/btg180

Rotllan-Puig X, Traveset A (2021) Determining the minimal background area for species distribution models: MinBAR package. Ecological Modelling 439: 109353. https://doi.org/10.1016/j.ecolmodel.2020.109353

Sciandra C, Mori E, Solano E, Mazza G, Viviano A, Scarfò M, Bona F, Annesi F, Castiglia R (2022) Mice on the borders: Genetic determinations of rat and house mouse species in Lampedusa and Pantelleria islands (Southern Italy). Biogeographia – The Journal of Integrative Biogeography 37(1): a013. https://doi.org/10.21426/B637155716

Setliff GP, Anderson JA (2011) First record of the agave snout weevil, *Scyphophorus acupunctatus* Gyllenhal (Coleoptera: Curculionidae: Dryophthorinae), in Puerto Rico. Insecta Mundi 152: 1–3.

Smith GF, Figueiredo E (2007) Naturalized species of *Agave* L. (Agavaceae) on the southeastern coast of Portugal. Haseltonia 13: 52–60. https://doi.org/10.2985/1070-0048(2007)13[52:NSOALA]2.0.CO;2

Smith AB, Alsdurf J, Knapp M, Baer SG, Johnson LC (2017) Phenotypic distribution models corroborate species distribution models: A shift in the role and prevalence of a dominant prairie grass in response to climate change. Global Change Biology 23(10): 4365–4375. https://doi.org/10.1111/gcb.13666

Soroker V, Colazza S (2017). Handbook of Major Palm Pests: Biology and Management. John Wiley & Sons, New York, 316 pp. https://doi.org/10.1002/9781119057468

Srivastava V, Roe AD, Keena MA, Hamelin RC, Griess VC (2021) Oh the places they'll go: Improving species distribution modelling for invasive forest pests in an uncertain world. Biological Invasions 23(1): 297–349. https://doi.org/10.1007/s10530-020-02372-9

Steen VA, Tingley MW, Paton PW, Elphick CS (2021) Spatial thinning and class balancing: Key choices lead to variation in the performance of species distribution models with citizen science data. Methods in Ecology and Evolution 12(2): 216–226. https://doi.org/10.1111/2041-210X.13525

Stüben PE, Schütte A, Astrin JJ (2021) Barcoding and interspecific relationships of Macaronesian Weevils (Coleoptera: Curculionoidea). Beiträge zur Entomologie, Contributions to Entomology 71: 127–135. https://doi.org/10.21248/contrib.entomol.71.1.127-135

Tamura K, Stecher G, Kumar S (2021) MEGA11: Molecular Evolutionary Genetics Analysis version 11. Molecular Biology and Evolution 38(7): 3022–3027. https://doi.org/10.1093/molbev/msab120

Thiede J, Smith GF, Eggli U (2019) Infrageneric classification of *Agave* L. (Asparagaceae: Agavoideae/Agavaceae): a nomenclatural assessment and updated classification at the rank of section, with new combinations. Bradleya 37(37): 240–264. https://doi.org/10.25223/brad.n37.2019.a22

Thompson AM, Singh HB, Stewart RW, Kucsera TL, Kondo Y (1997) A Monte Carlo study of upper tropospheric reactive nitrogen during the Pacific Exploratory Mission in the Western Pacific Ocean (PEM-West B). Journal of Geophysical Research 102(D23): 28437–28446. https://doi.org/10.1029/97JD02555

Thuiller W (2014) Editorial commentary on "BIOMOD – optimizing predictions of species distributions and projecting potential future shifts under global change. Global Change Biology 20(12): 3591–3592. https://doi.org/10.1111/gcb.12728

Valavi R, Elith J, Lahoz-Monfort JJ, Guillera-Arroita G (2019) blockCV: An R package for generating spatially or environmentally separated folds for *k*-fold cross-validation of species distribution models. Methods in Ecology and Evolution 10(2): 225–232. https://doi.org/10.1111/2041-210X.13107

Valavi R, Elith J, Lahoz-Monfort JJ, Guillera-Arroita G (2021) Modelling species presence-only data with random forests. Ecography 44(12): 1731–1742. https://doi.org/10.1111/ecog.05615

van Rossem G, van de Bund CF, Burger HC, de Goffau LJW (1981) Bijzondere aantastingen door insekten in 1980. Entomologische Berichten 41: 84–87.

van Vuuren D, Stehfest E, Den Elzen M, Kram T, van Vliet J, Beltran AM, Oostenrijk R, van Ruijven B (2011) RCP2.6: Exploring the possibility to keep global mean temperature increase below 2 °C. Climatic Change 109(1–2): 95–116. https://doi.org/10.1007/s10584-011-0152-3

Vassiliou V, Kitsis P (2015) First record of the sisal weevil, *Scyphophorus acupunctatus*, in Cyprus. Entomologia Hellenica 24(1): 22–26. https://doi.org/10.12681/eh.11542

Vaurie P (1971) Review of *Scyphophorus* (Curculionidae: Rhynchophorinae). Coleopterists Bulletin 25: 1–8.

Waring GL, Smith RL (1986) Natural history and ecology of *Scyphophorus acupunctatus* (Coleoptera: Curculionidae) and its associated microbes in cultivated and native agaves. Annals of the Entomological Society of America 79(2): 334–340. https://doi.org/10.1093/aesa/79.2.334

Supplementary material 1

Supplementary data

Authors: Andrea Viviano, Arturo Cocco, Paolo Colangelo, Giuseppe Marco Delitala, Roberto Antonio Pantaleoni1, Laura Loru

Data type: docx

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/neobiota.90.101797.suppl1